Bergmann's rule in skull size and shape of wild vs. captive *fascicularis*-group macaques

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Introduction

Bergmann's rule predicts that body size increases with latitude as colder temperatures favor larger bodies[1]. This pattern has been noted in the majority of wild mammal species, including macaques[2]. Wild *fasicularis*-group macaques (**Figure 2**) cover a full 45° of latitude (**Figure 1a**) and they are commonly kept in captive colonies at non-endemic locations (**Figure 1b**). Comparing the presence of Bergmann's rule in skull size and shape of wild versus captive macaques is an opportunity to investigate whether the pattern is influenced more by natural selection or developmental plasticity.

Figure 1a. Wild sample localities; colors and symbols as for Figure 3

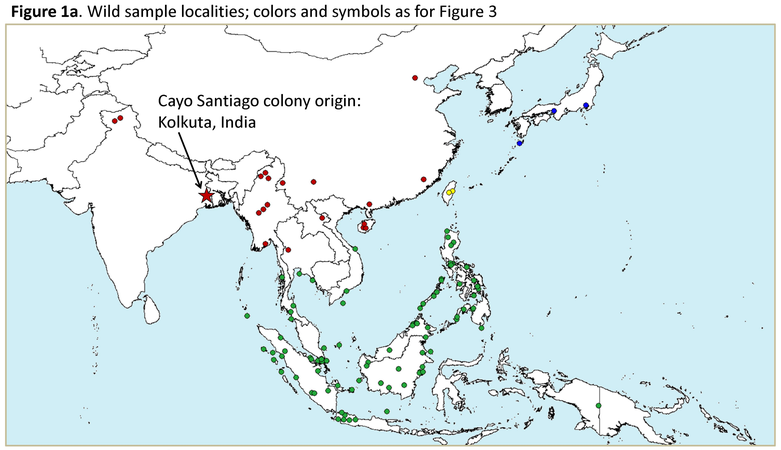
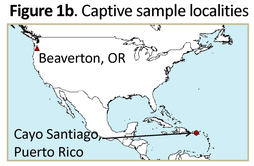


Table 1. Sample sizes for wild and captive populations

Species/ population	N (F/M)	Range (degrees latitude)
M. fascicularis	188 (73/115)	-7.0 - 18.5
M. mulatta	29 (17/12)	15.9 - 39.2
M. fuscata	17 (5/12)	30.3 - 35.7
M. cyclopis	13 (5/8)	23.7 - 23.9
Cayo Santiago, Puerto Rico	40 (20/20)	18.2
Beaverton, OR	18 (7/11)	45.5

Figure 1b. Captive sample localities



Materials and Methods

- Forty-five 3D cranial landmarks collected with a Microscribe 3D-X, following Frost et al.[3]
- Sample of 247 adult wild *fascicularis*--group macaques and 58 adult captive *M. mulatta* from Cayo Santiago and Beaverton, OR (**Table 1**)
- Cayo Santiago colony founded in 1938 with populations from Kolkuta, India (lat= 22.6)[4]; Beaverton, OR founded 1964 from India and China[5]
- Natural-log transformed cranial centroid size used as a proxy for body size
- Covariation between geographic and shape coordinates examined with a two-block partial least squares analysis (2B-PLS). Variance due to sex is not included in the scores, thus predictions are based on pooled sex correlations only. The first geographic vector defined northern vs. southern morphotypes (**Figure 5**)
- Natural log of the centroid sizes and 2B-PLS scores plotted against absolute value of latitude, mean annual rainfall, and mean annual temperature
- Regression analyses for size and shape with latitude used to calculate predicted values for pooled sex, males, and females each within total wild sample and *M. mulatta* only sample (**Tables 2a and 2b**)

Figure 2. From left to right: *M. mulatta*, *M. cyclopis*, *M. fuscata*, *M. fascicularis*

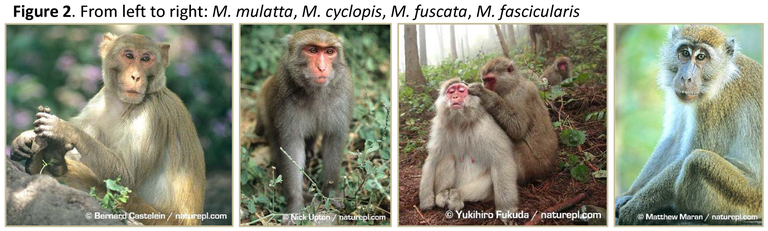


Figure 3. Absolute value of latitude and natural log of centroid size. Males are solid shapes, females are open shapes.

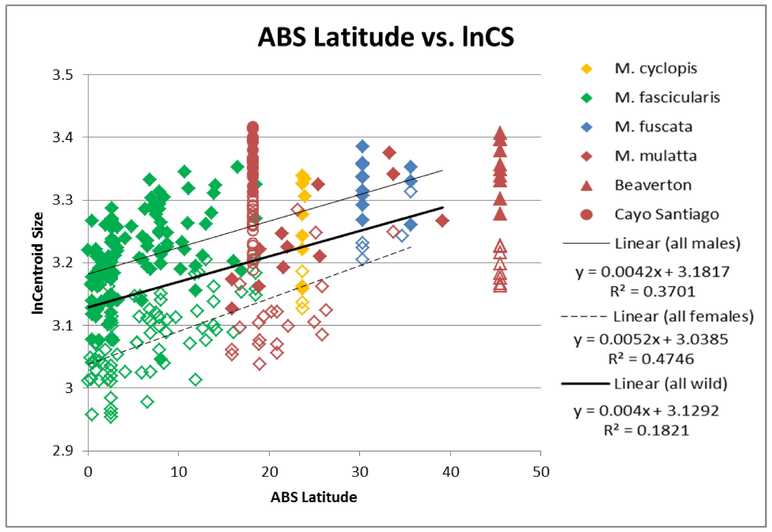
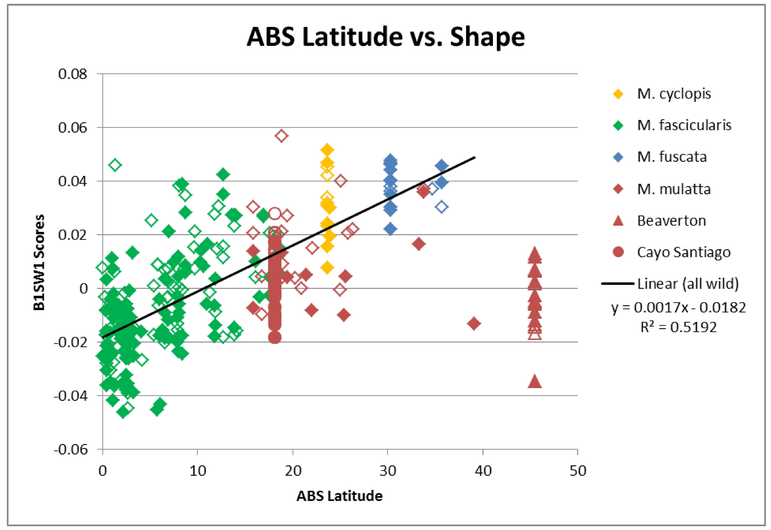


Figure 4. Absolute value of latitude and 2B-PLS shape scores. Males are solid shapes, females are open shapes.



Results

- Wild *fascicularis*-group macaques: location significantly correlated with size (males R^2=0.37, p=0.00; females R^2=0.47, p=0.00; **Figure 3**) and shape (pooled sex R^2=0.51, p=0.00; **Figure 4**)
- Temperature significantly correlated with size (males R^2=0.23, p=0.00; females R^2=0.26, p=0.00) and shape (pooled sex R^2=0.24, p=0.00)
- Wild *M. mulatta* only: location significantly correlated with size (males R^2=0.59, p<0.003; females R^2=0.34, p<0.005) but not shape (pooled sex R^2=0.009, p=0.62)
- Captive male skull sizes not significantly different between locations (p>0.20), but Cayo Santiago females significantly larger than at Beaverton (p<0.005)
- Entire captive samples not significantly different from each other in size (p>0.10), but were in shape (p<0.05)
- Expected latitudes based on entire wild sample (**Table 2a**) and *M. mulatta* only (**Table 2b**) clines presented below

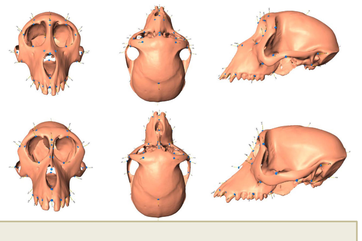
Table 2a. Expected latitudes based on total wild cline

	Beaverton	Cayo Santiago
Male size	40.7	44.8
Female size	30.5	41.5
Pooled size	36.1	45.3
Shape	8.4	13.3

Table 2b. Expected latitudes based on *M. mulatta* only cline

	Beaverton	Cayo Santiago
Male size	39.8	42.6
Female size	30.3	37.7
Pooled size	34.0	37.7
Shape	n.s.	n.s.

Figure 5. Shapes defined by ends of first geographic vector (above: northern; below: southern). Left to right: frontal, dorsal, lateral views



Discussion

Bergmann's rule originally related body size and temperature[1], but the results suggest temperature alone is not driving size in wild macaques. Within the wild macaque sample, both skull size and shape were more significantly correlated with latitude than temperature. Mean annual rainfall was not correlated with skull size (R^2=0.006), and mean annual temperatures are approximately constant for the bulk of the sample localities, from approximately -10° to 20° latitude.

Males were predicted to be more northern than females based on their size for both captive populations, and Cayo Santiago specimens were predicted to be more northern than Beaverton specimens by both size and shape. Compared to size, shape scores predicted captive populations to come from considerably lower latitudes than either their current captive locations or their original populations would predict. The size and shape results of the captive specimens together suggest that while the captives are much larger than their wild latitudinal counterparts, their skull shape reflects the more southern condition.

The Cayo Santiago macaques are a provisioned free-ranging colony, and they also forage the natural vegetation on the island[4]. The Beaverton macaques are not free-ranging, and their only food source is provisioned. The larger Cayo Santiago females compared to the Beaverton females may be a result of increased feeding competition. Phenotypic plasticity likely plays an important role in the latitudinal pattern, and investigating more correlates of size and shape in *fascicularis*-group macaques may help explain the drivers of Bergmann's rule.

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Citations

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Figure 2 pictures from arkive.org